Antlions' Group Distribution and Behavior under Varying Spatial Constraints

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Source: `https://git.hrhr.dev/scifair`

Abstract

Emergent group behaviors were observed which point toward a certain degree of cooperation by antlions. The donut theory, the forerunner in describing antlions' spatial distribution, asserts that the insects form a ring to capture ants approximately equitably. Similar "cooperative" behavior was observed, with the antlions remaining under the soil when the surface was overpopulated (demonstrable by a significantly lower number of pits forming in smaller trials). The donut theory was confirmed by the observed spatial distribution because antlions often stuck to the side of the trial area despite there being significant available space on the inside of the circle where an individual could gain competitive advantage. The hypothesis that they exhibit more extreme behaviors under space constraints was confirmed because, proportional to the number introduced, especially in the 8x7 trial, cannibalism and non-formation of pits increased significantly—likely as a compensatory mechanism to ensure that a stable "surface group" could still safely exist. Additionally, territory (measurable by the Voronoi diagrams and by nearest-neighbor) decreased towards the later trials, and the patterns didn't merely display the same structure scaled down—rather, antlions accepted more dense conditions by increasing pit density. This likely corresponds to natural conditions (especially in hatcheries) where some proportion of the antlions remain on the surface (increasing with population density because it's understood to mean a prevalence of food), and as the surface antlions become adults (sometimes fed through cannibalism), new larvae emerge to take their place and sustain the species' propagation.

Introduction:

Throughout the animal kingdom, animals have been constantly competing for limited resources across limited amounts of space. The interaction between animals of the same and different species is the focus of numerous scientific disciplines, but the focus of most has been mammals and other complex species rather competition within species like insects. Rather than focus on the effect of spatial constraints an organism with complex brain and social hierarchy the study aimed to focus on a smaller and less complex organisms to determine if the same spatial patterns that appear with mammal groups still appear as an emergent result of environmental pressures, which is demonstrably true if antlions also display similar behavior. On the basis of this, it was examined as to how antlion pattern themselves in groups, namely by measurement of how pit depth, width, and nearest neighbor and behavior, such as cannibalism and temporary reclusion, vary with respect to spatial constraints and temporal change. Through prior investigation and research it was determined that antlions generally tend to avoid highly aggressive competition and likely form semi-hexagonal patterns to evenly distribute resources across the population (given that each individual could only consume so many ants). However, it was determined that antlions sometimes exhibit extreme behaviors such as cannibalism and reclusivity when under significant environmental pressure. The preliminary research provided background for the following hypothesis: "As the space available to antlion groups decreases, each claims less territory, and the populations tend towards more extreme behaviors, such as cannibalism and reclusivity, to limit competition for ants as an emergent feature of individual interactions." Throughout the experiment several dependent variables were tested, with the independent variable acting as the size of the container, which changed from trial to trial, but did not change due to any other variable. In continuation of this, the dependent variables throughout the experiment were the settlement patterns and behaviors of the antlions, which were quantified through the nearest neighbor calculation, pit depth and width, and the number of cannibalized antlions. The control trial of the experiment was the 32x32 trial, as it shows the spatial patterns and behaviors of the antlions with the most available space, limiting the effect of competition on settlement patterns, which qualifies it to be a good control group.

Background Research:

To design the experiment and understand the organisms' underlying behaviors which might affect it, extensive background research was required—specifically on their spatial distribution patterns. First, a previous study analyzing the spatial patterning and structure of termite mounds in an African savanna was examined to better understand the procedure of the experiment. This study examined how different termite colonies in the African savanna positioned themselves in relation to one another, and uncovered that termite mounds each neighbor sic other termite mounds at a relatively constant distance, creating uniform hexagons of termite mounds through the savannah. Furthermore, this study uncovered that termite mounds must maintain a constant distance from each other to prevent conflict between termite colonies, which would limit the overall success of the species. These results helped guide and shape this study that was conducted by providing insight to the possible intraspecies competition that could result from close antlion contact, leading to the prediction that antlions (Myrmeleon immaculatus) would have to space themselves in order to prevent competition for food. Lastly, this study determined that a change in available space could affect the spatial patterns of termites as well as their behavior, which was later used in designing the conducted experiment.

Next, several studies regarding the anatomy and behavior of antlions were used in order to better understand the insects. These studies determined that antlions stay in their larva form, in which they make pits, for 6-8 weeks and develop slower when exposed to less food. This helped determine the timeline of the experiment and determine the intervals at which the antlions would be fed, as in order to keep results consistent the antlions would have to be the same throughout the course of the experiment, which would require the participating antlions to be fed less in order to stay in their larva stage to make pits. Furthermore, these studies examined terms such as pit depth and width as well as the feeding patterns and behaviors of antlions, which became crucial areas of study throughout the experiment, as these studies determined that pit depth and width can signify the dominance and success of antlion settlement. This helped determine the dependent variable—size/density constraints—to examine over the course of the study. Finally, these studies determined that antlions have a tendency to cannibalize each other in times of food shortage and significant competition. This provided another dependent variable to track over time and examine as size decreased, as cannibalized antlions were unsuccessfully metabolized and evident in pits.

Lastly, a series of studies about antlion dispersal pattern called the "Doughnut theory" were examined to better understand the current scientific knowledge surrounding antlion dispersal patterns. These papers determined that antlions naturally position themselves in a "doughnut," in which a ring of antlions circle a center point or food source to limit competition for ants, as each antlion has equal access to the food source. This study also concluded that when antlions are introduced one by one the same results occur, which confirmed that the procedure could introduce one antlion at a time without interfering with results and spatial patterns, helping further perfect and standardize the procedure, as well as provide a better understanding of antlions behavior patterns. These studies provided a better understanding of antlion settlement patterns and gave a guideline for what to expect as trials continued. Finally these studies provided scientific procedures that could be tested and confirmed throughout the experiment, allowing for a source to cross-check results and procedures with in order to perfect the procedure of the experiment.

Procedure:

Once materials were obtained the 160 ants were kept in one of the 6 inch plastic containers, and 200 grams of native sand was poured into each of the 40 remaining six inch containers. Next, each of the 40 antlions (Myrmeleon immaculatus) were placed in one of the plastic containers containing sand, with each antlion getting its own container. Following this each noticeable antlion pit was given two ants as food once every week, starting the Friday after the antlions were introduced to their temporary containers. Then, the remaining amount of sand was placed into the 32x32 container and spread out using a meter stick until the surface of the sand was level. Next, a meter stick was used to mark the sides of the 32x32 container with inch markers starting from the bottom right of the container on its lid. Much like a coordinate plane, marks were made one inch apart going vertically from the bottom of the lid of the container and subsequently labeled with their position away from the bottom of the box in inches, this acted as the y-axis. After this, marks were made one inch apart going horizontally from the right most section of the lid of the container and subsequently labeled with their position away from the right of the box in inches, this functioned as the x-axis. Next, the 2 inch cup was placed at the center of the container and buried under 3cm of sand. After this 4 antlions were introduced to the container every 24 hours until 30 antlions had been introduced, starting at 3:30 pm. This was done by using the sieve to obtain four random antlions from their temporary containers and place them on the center of the container, where the plastic cup was. Antlions were moved by using the sieve to remove the antlion from its six inch holding container. As new antlion pits appeared toothpicks were inserted next to them to signify their presence. Following the introduction of all 31 antlions a 24 settling period was allotted, after which the location of each antlion was measured using the grid system created earlier. Following this a program was used to find the nearest neighbor and a ruler was used to find the pit depth and width in cm. After data was taken the antlions were transferred back to their temporary containers by using a sieve to obtain the antlions from pits, where they were later placed in their temporary containers, dead antlions were kept in a freezer. Following this a barrier was inserted to reduce the available space to 24x23 inches using cardboard dividers and sealed using making tape, to prevent antlions from escaping the enclosure. After this another hour introductory period every 24 hours was repeated, will all remaining antlions, as some died in the previous trial. Once all antlions were introduced another 24 hour settling period was allocated and pit depth, width and location were found using the same methods as above, and the antlions were returned to their temporary containers. Following this the area of the box was reduced to 16x15 inches and all antlions were again introduced, 4 every 24 hours until all remaining antlions were placed in the pit. Then another 24 hour settlement period was allotted and all data was collected the same was as the previous two trials, and the antlions were returned to their temporary containers. Lastly, the area of the box was reduced to 8x7 inches and all antlions were again introduced, 4 every 24 hours until all remaining antlions were placed in the pit. Then another 24 hour settlement period was allotted and all data was collected the same was as the previous three trials, and the antlions were returned to their enclosures. To further understand the relevance of the study, the species of the antlions were examined through DNA barcoding. Using min PCR and a gel barcoding system the antlion DNA was extracted, and used a strand of mitochondrial DNA, cytochrome C in order to identify the antlions using a national protein database. The observed genus and species was Myrmeleon Immaculatus.

Materials:

First, a 32x33 container was used to house antlions. A cardboard barrier (and sufficient tape) was constructed to restrict it to a 24x24, 16x17, and 8x7 spaces. Approximately 200 pounds, or four 50lb bags, of quartz sand were needed as a substrate. Next, 40 antlions were obtained and 160 ants for food. 40 plastic circular containers (at a six inch diameter and a four inch depth) housed the antlions and 1 housed the ants. One meter stick, a six inch ruler, and a sharpie were obtained to measure and obtain data from trials. Then, 40 toothpicks and a small plastic cup with a diameter of 2 inches were applied to record and manage the locations of antlions throughout the study. A sieve was used to move the antlions from place to place and secure them.

Data Analysis:

The patterns created by antlion groups are emergent: they don't exhibit top-down structure like a highly regular tiled or even consistent polymorphism across trials. However, the antlions (Myrmeleon immaculatus) did cluster somewhat (remaining close to each other despite available space, in some cases) but regardless maintained sufficient area to capture food, either of the cannibalistic or regular sort. These patterns likely developed, at least in the short terms these antlions were studied, by slow movement of the pits across the trial area, either by live migration or abandonment of old pits (which often occurred). The Voronoi diagrams are the primary source which exhibits these traits: scaled down to the window of the trial area which antlions populated, the area claimed by each individual antlion is somewhat consistent, explicable by a selfish algorithm:

each antlion wants to optimize its area of ant capture (represented by “claimed” regions on the Voronoi diagrams), so the area was shared about equally by the group. Also, average distance to nearest neighbor decreased with lesser trial area: from 5–6cm on average in the 33x32cm trial down to 3–3.5cm in the 8x7cm trial, the graph in Figure 3 demonstrates a clear correlation, with a notable (but inconclusive) p-value of about 8%, between territorial area and total area. Additionally, compensatory behaviors were exhibited which further managed the population: cannibalism and reclusion both prevented surface overpopulation (because when two antlions were too close, one or the other usually occurred).

On the scale of individual pits, antlions optimize for energy. Unrelated to their partners’ pits size, antlions typically size their pits to capture ants. Weekly feedings helped maintain the natural analogue to scarce ant feedings, so the antlions had to create their pits as determined by the density of the environment (simulated by a small area, which antlions readily detected despite their blindness by extensive trails created in the container). This caused them to create significantly smaller pits (so much so that at about .8cm deep and .8cm wide, measurement errors became excessively significant) in smaller containers (in terms of depth and width) because the antlions were aware that ants would, regardless, fall in rather than survive throughout the antlion colony. This is in contrast to the 33x32 where none of the antlions formed pits shallower than 1.1cm and one pit was 4.2cm wide. Furthermore, large pits may have become an unnecessary aggression or warning mechanism because, in order to preserve the larvae, the species would require sufficiently clear land that a group could populate the surface fully without unintentionally increasing cannibalism rates.

Throughout the study a clear increase in extreme behaviors was noted, which is shown by Table 1 (Appendix B, Figure 4), which shows that the initial 33x32 trial size had a 19.35% fatality rate among the 31 antlions involved in the trial, compared the last 8x7 trial size which had a 33.33% fatality rate. This resulted in a 13.9785% increase in deaths throughout the study, which falls within a p value of below 0.05, making the results statistically significant. The increase in deaths point towards increased cannibalism within the competing antlion population, as all deceased bodies were found with no head or appendages, but rather just a hard exoskeleton, leading to the conclusion that the antlions were cannibalized. The observed cannibalism of antlions supported the hypothesis that extreme behaviors would increase as trial size decreased, as antlions are known to resort to cannibalism in times of environmental and biological stress. Furthermore, the increased cannibalism was most likely a result of increased one one interactions between antlions within a smaller trial groups, as the antlions in smaller trial groups have less space to settle in, increasing the chances that they will come into contact with another antlion. Increased cannibalism could also have been a result of increased competition at lower trial sizes, as in lower trial sizes food was not as spread out as much as it was in larger trial sizes, which could result in increased competition, leading to aggressive behavior such as cannibalism. Furthermore, extreme behavior such as reclusivity, measured in the total antlions without pits, barely changed in relation to the total antlions introduced in the trial, as a reclusivity percentage of 29.03% was noted in the 33x32 trial, and a reclusivity percentage of 25% was noted in the 8x7 trial (Appendix B, Figure 4), which is not statistically significant change. This led to the conclusion that as trial size decreases aggressive behavior such as cannibalism increases, however, pacifistic behaviors such as reclusiveness are not affected. However, because the total amount of pits observed in each trial decrease as trial size decreases, it is possible that antlions keep a ration between the total amount of available territory and the number of active pits to avoid competition, as mentioned above in the territory calculation.

Both sets of behavior—extreme interactions like high levels of reclusivity or cannibalism and the spatial patterning of antlions under space constraints—are useful in models of the natural environments and behavior of antlion larvae. Reclusivity, for example, is an evolved behavior intended to allow as many larvae as possible to become adults as quickly as possible: rather than spread the wealth of ant food across a very large population, a partial proportion surface and would become adults within a matter of weeks. This is a protection mechanism against predators, and makes sense for the individual: reclusive behavior underground usually doesn't lead to death and below a certain threshold of energy intake, a pit on the surface doesn't make sense—especially considering the cannibalism risk. Cannibalism is partially an accidental behavior, but could certainly have some evolutionary implications: if the food supply runs low, antlions will move more and more antlions will be consumed by their peers to make up for the food supply. Furthermore, the increased surface density under more dense conditions, simulated by a small trial area, (rather than constant density with increasing reclusivity) means that antlions use population density as a proxy for food density because in nature, it would mean the area can support sufficient surface-dwellers. Antlions' behavior in the artifically constrained trial areas models closely their behavior in densely populated, constantly recycling nurseries, which explains the lack of highly regular structure.

Conclusion:

Pit depth and width correlate strongly with trial area, as demonstrated by graph one, which relates the two. The pit positioning of antlions (as a group and as individuals) likely varies solely to maximize ant capture. Therefore, this phenomenon is observed because antlions' (myrmeleon immaculatus) pits don't need to be as big when the main constraint on ants falling into the pit is simply having a pit available for them to fall into. This is also observable by the trials' decreasing number of visible pits (versus total antlions introduced) with respect to size: they start to hide underground because rather than simply having smaller pits than stronger antlions, they have to rest underground, possibly to preserve group wellbeing. Graph 2 indicates a similar trend—antlions' territory as described by the nearest neighbor calculation is much lower in smaller containers. This is the natural consequence of less area being available but demonstrates that the effects of hiding don't completely level the density of antlion pits based on population per area. Additionally, deaths remain minimal even in highly crowded conditions like the 8x7, which means that deaths are probably accidental at worst and antlions work to preserve the group's chances of surviving. The earlier hypothesis was proven to be correct, as the correlation between a smaller trial size and more extreme behaviors (such as cannibalism and reclusiveness) is supported by the data, as an increase in cannibalism was seen in lower treatment groups, hinting towards more aggressive behavior at lower trial groups, thereby proving the hypothesis.

Appendix A: Graphs:

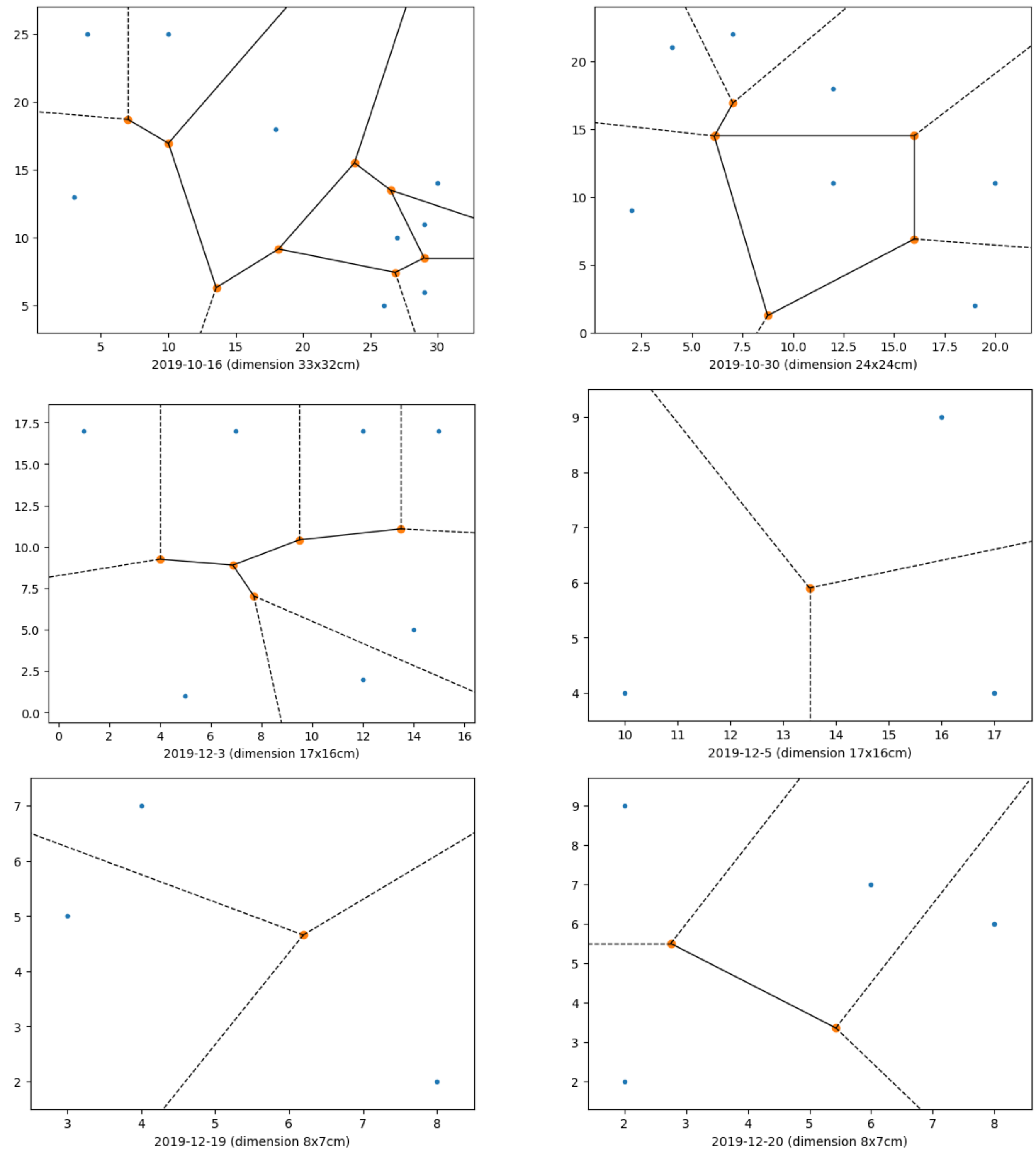

Fig 1: Voronoi diagrams showing the territory of each antlion that formed a pit and well as the location, depth, and width of each pit

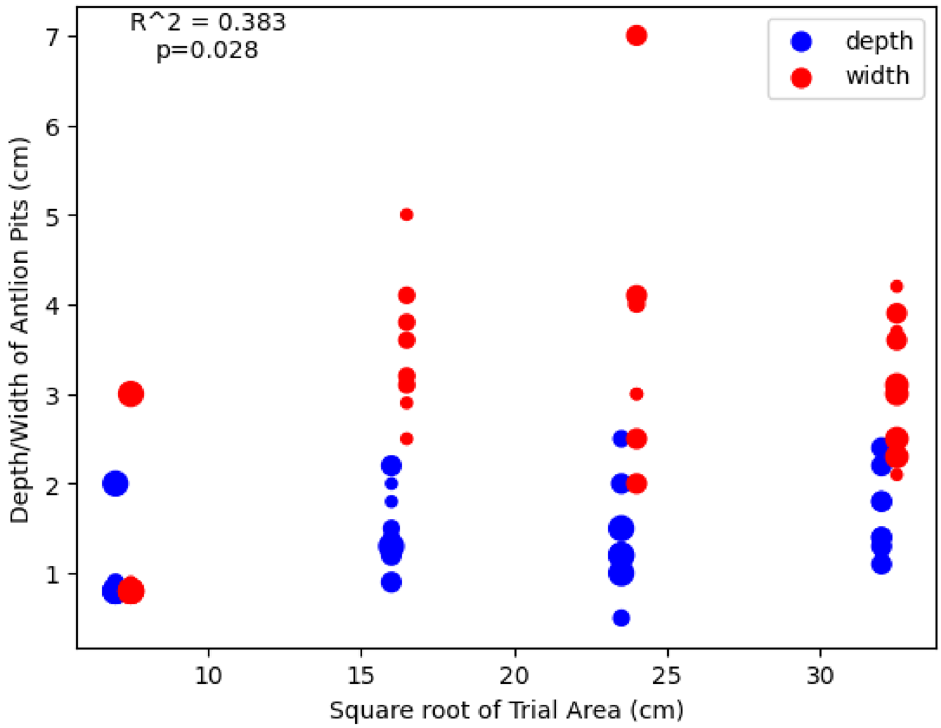

Fig 2: Shows pit depth and width in relation to the square root of the trial area

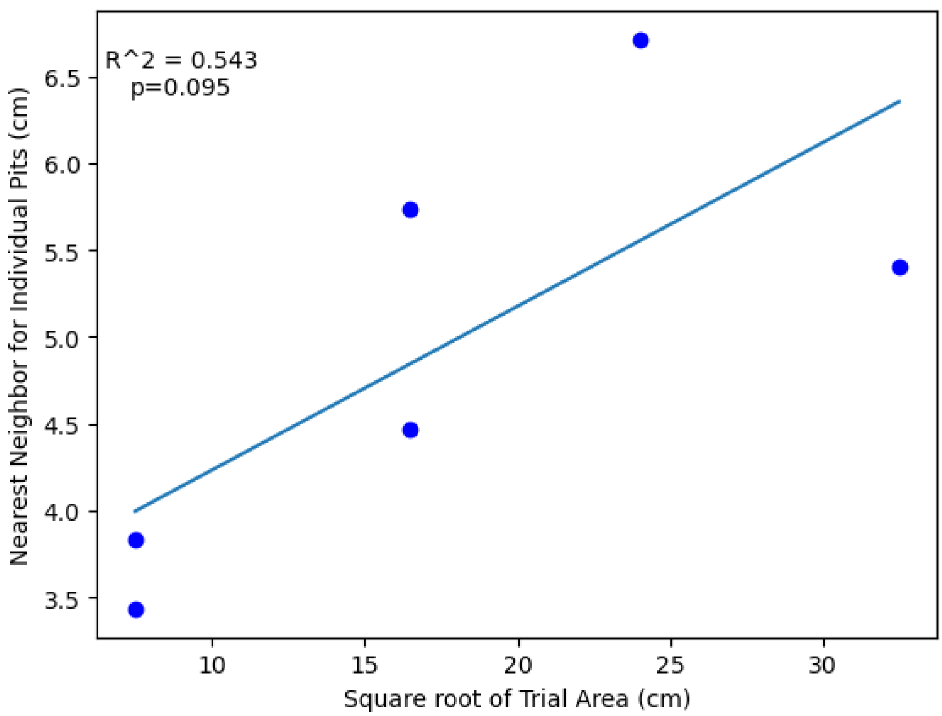

Fig 3: Shows the average nearest neighbor calculation for each trial group in relation to the square root of trial area, to create a ratio. Larger dots means more pits had that same area and depth or width.

Appendix B: Tables:

Trial Size	Date	Introduced	Deaths	Pits formed
33×32	2019-10-16	31	6	9
24×24	2019-10-30	27	3	7
17×16	2019-12-3	19	3	7
17×16	2019-12-5	10	0	3
8×7	2019-12-19	12	4	3
8×7	2019-12-20	5	0	4

Fig 4: Number of Deaths and Pits Successfully Formed in Each Trial/Subtrial

Dimensions (in)	Pit Depth (cm)	Pit Width (cm)	Nearest Neighbor (cm)
33×32	1.3	4.2	6.00
	1.4	3.7	12.04
	1.1	3.0	6.00
	1.8	2.3	10.63
	2.2	3.1	3.16
	1.4	2.5	2.24
	1.2	2.1	2.24
	2.4	3.9	3.16
	1.8	3.6	3.16
24×24	2.0	7.0	3.16
	2.5	4.1	3.16
	0.5	2.0	10.20
	1.2	2.5	6.40
	1.2	3.0	7.00
	1.0	3.0	8.00
	1.5	4.0	9.06
17×16	1.3	4.1	3.61
	1.2	3.8	3.61
	0.9	3.2	7.07
	2.2	3.8	3.00
	1.2	2.5	3.00
	2.0	5.0	5.00
	1.8	3.6	6.00
17×16	1.3	3.1	5.10
	1.5	3.1	7.00
	1.4	2.9	5.10
8×7	0.8	0.9	2.24
	0.9	0.8	2.24
	2.0	3.0	5.83
8×7	0.8	0.8	2.24
	0.8	0.8	6.40
	0.8	0.8	2.24
	0.8	0.8	4.47

Fig 5: The Pit Depths, Widths, and “Territory,” Observed in Each Trial

Appendix C: Pictures:

Fig 6: Pictures of the 32x33 trial group, a six inch ruler is shown for scale.

Fig 7: Initial pictures of the 24x25 trial group including the new cardboard barrier for reference.

Fig 8: (Left) A photograph of the first 16x17 trial, note antlion trails that are shown, a six inch ruler is shown for scale. (Right) A picture of the reinforced cardboard barrier to prevent antlions from escaping.

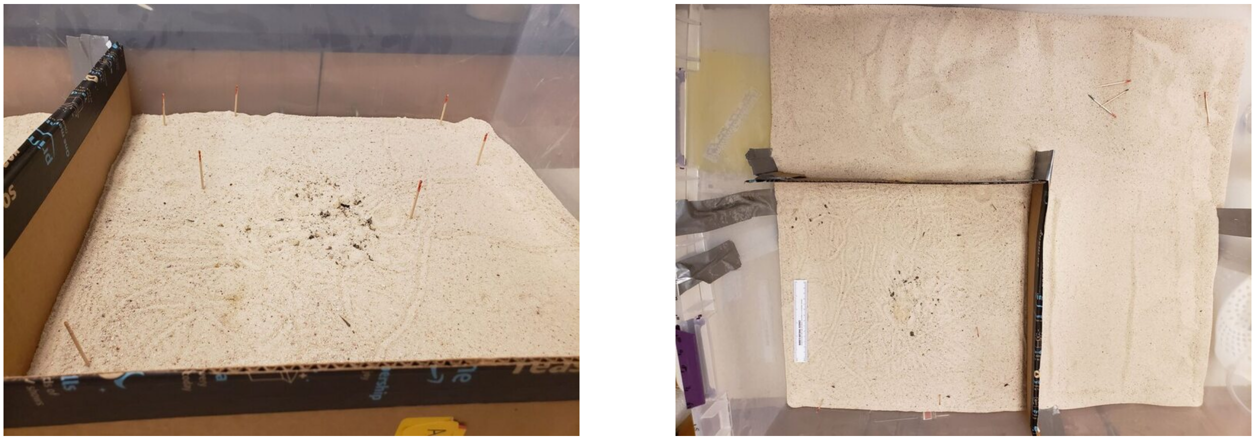

Fig 9: Two alternate views of the 16x17 trial size, note antlion trails and toothpicks denoting the location of antlion pits.

Fig 10: (Left) A close up image of the 16x17 trial size, note pits and dead antlions, ruler shown for scale (Right) A close up image of the 8x9 trial size, note smaller and less consistent pits, a six inch ruler shown for scale

Fig 11: (Left) A picture of an antlion being removed from the trial period (Right) An image of an antlion in its temporary container

Bibliography

Muvengwi, J., Davies, A. B., Parrini, F., & Witkowski, E. T. F. (2018). Geology drives the spatial patterning and structure of termite mounds in an African savanna. Ecosphere, 9(3), e02148. https://doi.org/10.1002/ecs2.2148

Bowen*, T., Cabello*, G., Gidden*, T., Schlueter, M., & Cain, P. (2019). BIOTIC AND ABIOTIC FACTORS INFLUENCING ANTLION PIT PLACEMENT **. Georgia Journal of Science, 77(1). Retrieved from https://digitalcommons.gaacademy.org/gjs/vol77/iss1/72

Barkae, E. D., Golan, O., & Ovadia, O. (2014). Dangerous neighbors: Interactive effects of factors influencing cannibalism in pit-building antlion larvae. Behavioral Ecology, 25(6), 1311–1319. https://doi.org/10.1093/beheco/aru123

Scharf, I., Hollender, Y., Subach, A., & Ovadia, O. (2008). Effect of spatial pattern and microhabitat on pit construction and relocation in Myrmeleon hyalinus (Neuroptera: Myrmeleontidae) larvae. Ecological Entomology, 33(3), 337–345. https://doi.org/10.1111/j.1365-2311.2007.00967.x

Crowley, P. H., & Linton, M. C. (1999). Antlion Foraging: Tracking Prey Across Space and Time. Ecology, 80(7), 2271–2282. https://doi.org/10.1890/0012-9658(1999)080[2271:AFTPAS]2.0.CO;2

A. S Erasmus, B. F. N. *. (2000). A modelling approach to antlion (Neuroptera: Myrmeleontidae) distribution patterns. African Entomology, 8(2), 157–168.